

Small-Scale Dispersion of Eggs and Sperm of the Crown-of-Thorns Starfish (*Acanthaster planci*) in a Shallow Coral Reef Habitat

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Abstract. The dispersal of eggs and sperm of crown-of-thorns starfish, *Acanthaster planci* (L.), was measured in the field using an array of collectors up to 10 m downstream of a spawning starfish. Hydrodynamic measurements, gamete dispersal numerical models, and the gamete cloud dispersal measurements for the first time quantified the relationship between hydrodynamic conditions and the dispersion of eggs and sperm in the field. In general, gamete concentrations fell rapidly and logarithmically with distance from the spawning starfish; egg concentrations at 3 m were 1% of those near the starfish. Simplified dispersal models showed a good correspondence with these field data, and confirmed the observation that eggs rose higher in the water column and spread more laterally at low current speeds over the short spatial scales being considered.

Fertilization rates, predicted from laboratory measurements of fertilization success and the gamete concentrations measured in the field, were estimated to be 90–100% within 1 m and 70–100% at 10 m. These results are explained by high success rates of fertilization (fertilizing capacity) at the measured dilutions, and were similar to fertilization rates previously measured by others for crown-of-thorns starfish in the field.

Although the eggs were observed to spread upwards into the water column due to turbulence, laboratory measurements of sinking rates showed eggs to be very slightly negatively buoyant (median fall velocity of $0.072 \text{ mm} \cdot \text{s}^{-1}$), whereas sperm were neutrally buoyant. A significant fraction of eggs also entered the seabed near

the starfish; the proportion decreased with increasing current strength. This process may provide a mechanism for enhanced fertilization of these gametes and/or a mechanism for self-recruitment to a given reef population.

Introduction

Many marine organisms release their gametes into the seawater where fertilization takes place. Theoretical (Vogel *et al.*, 1982) and laboratory (Lillie, 1915, 1919; Cohn, 1918; Gray, 1928; Levitan *et al.*, 1991) studies have demonstrated that gamete concentration plays a key role in the fertilization success of such organisms. This results not only from changes in the probability that gametes will encounter each other, but also from the marked decrease in fertilizing capacity of sperm with increasing dilution (Gray, 1928; Chia and Bickell, 1983).

Illustrative models of the effects of turbulent flow have demonstrated the dominant effect fluid dynamics are likely to have on gamete dispersion and on the likelihood of successful fertilization (Denny, 1988; Denny and Shibata, 1989). Dispersal of gametes at reef scales has been examined (*e.g.*, Black *et al.*, 1991). However, despite the importance of the interaction of gametes and the fluid environment, no experiments have been undertaken at small spatial scales to link the physics of the water body to the measured dispersal of gametes in the natural environment. Such information is of vital importance to understanding the dynamics of external fertilization.

The few field studies of fertilization that have been carried out in sea urchins (Pennington, 1985), hydroids (Yund, 1990), and ascidians (Grosberg, 1991) have all confirmed theoretical predictions (Denny and Shibata,

1989) that fertilization rates drop rapidly with distance from the spawning adult. Pennington (1985) found the proportion of sea urchin eggs fertilized by sperm in seawater sampled at different distances downcurrent of a spawning male was above 60% over 0.1 m, falling to 15% over 0.2 m and to less than 5% over 1 m. Sperm dispersal estimated in ascidians from the spread of genetic markers showed that 20–40% of embryos within 0.05 m of a male source had been fertilized by that male, but that less than 5% had been fertilized over 0.5 m away (Grosberg, 1991). In marine hydroids, fertilization rates were more than 80% within 3 m of the male source, but dropped to zero at distances greater than 7 m (Yund, 1990). The reproductive success of female octocorals, *Briareum asbestinum*, was also greater the closer they were to males and in hydrodynamic conditions where dilution of sperm was likely to be less (Brazeau and Lasker, 1992). This implies that the magnitude of the spatial separation of spawning individuals is crucial to the fertilization success achieved. These data suggest that the aggregation of many species during spawning is a mechanism to enhance fertilization success (Pennington, 1985).

In marked contrast, high fertilization rates have been measured over tens of meters from spawning male crown-of-thorns starfish (Babcock and Mundy, 1992). This result might reflect the large number of gametes released by this starfish (diameter up to 0.5 m) and the fact that individuals are widely dispersed in their natural habitat. Up to 10^8 eggs are produced per female (Birkeland and Lucas, 1990), and up to 140 ml of sperm (Babcock and Mundy, 1992)—at densities of up to 8×10^8 sperm ml^{-1} (Benzie and Dixon, 1994)—are produced per male, although densities may be much lower once the sperm is released into a moving water column. Although there are reports of aggregations of starfish during spawning, these have been observed only in high-density outbreaking populations (Birkeland and Lucas, 1990). The species normally occurs in much lower densities (Moran and De'ath, 1992), which suggests that gamete dispersal needs to be effective.

The influence of water flow has been recognized in all the field studies of fertilization. Differences in the dispersal of sperm inferred from population genetic structuring of ascidian populations at sites in the United States and Italy were thought to be the result of the different flow regimes at the two locations (Grosberg, 1991). The site with slow currents had limited sperm transfer, whereas the site with fast, highly turbulent flows had population structures consistent with sperm dispersal over greater distances. Research by Pennington (1985) showed that the fertilization of eggs was greatest, over distances of 1 m, when current speeds were low (*i.e.*, $< 0.2 \text{ m} \cdot \text{s}^{-1}$). The potential effects of hydrodynamic conditions on fertilization success have also been noted in reef fish (Peterson, 1991), octo-

corals (Brazeau and Lasker, 1992), and scleractinian corals (Oliver and Babcock, 1992). However, no previous studies have measured the dispersal of the gametes themselves or obtained simultaneous information on current flows, turbulence, and boundary conditions that might have better described the conditions in which the measured fertilization rates were achieved.

The aim of the present work was to establish the dispersion patterns of eggs and sperm of the crown-of-thorns starfish in the field, and to determine the link between gamete dispersion patterns and the physics of the natural environment.

Materials and Methods

Field experiments

Experiments were conducted at Little Broadhurst Reef in the Central Section of the Great Barrier Reef (Fig. 1) along a 40 m \times 10 m transect established on a large patch reef within the lagoon. Natural concentrations of eggs and sperm downstream of a spawning starfish were determined using a vertical array of nineteen 12-V bilge pumps (Fig. 2) set into a mobile frame that could be moved up to 10 m downstream of the starfish. Sixteen pumps were arranged at the nodes (450–500 mm apart) in a rectangular

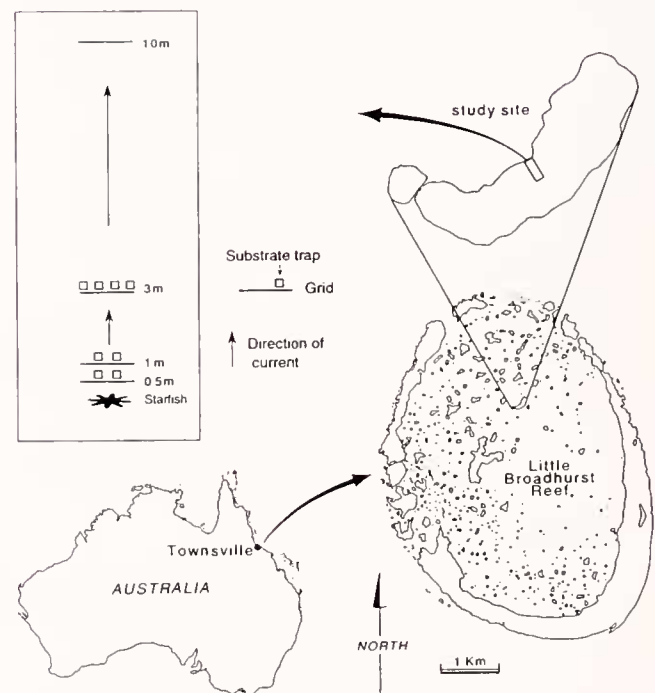


Figure 1. Map showing the location of the experimental site on Little Broadhurst Reef in the Great Barrier Reef, and the setup of the pump array and substrate traps within the study transect relative to the spawning starfish.

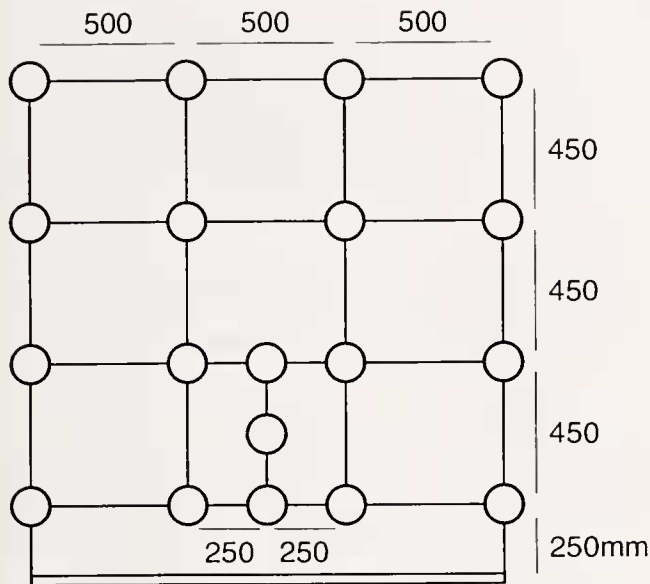


Figure 2. Plan of the pump array.

grid. To improve resolution over the shorter distances, three additional pumps were set about 250 mm apart in the lower middle section of the frame (Fig. 2). Another pump positioned next to the starfish measured the concentration of gametes being released. All pumps were connected by 30-m-long, 12-mm-diameter plastic hoses to filters located on a moored barge. Pumping rates were approximately $2 \text{ l} \cdot \text{min}^{-1}$.

Up to six "substrate" traps were deployed downstream of the starfish to measure the number of eggs lost to the seabed (Fig. 1). Each trap consisted of a small plastic tray ($0.13 \times 0.13 \times 0.05 \text{ m}$) filled with moderate-sized pieces of clean, angular pieces of rock, 20–30 mm in diameter. The rock was added to provide substrate with a porosity similar to that of the natural seabed and to provide a similar hydrodynamic environment. Normally two traps were deployed at 0.5 m and 1 m from the starfish, and a further four traps were deployed at 3 m. During Experiment 6 when the current speed was very slow, the four traps from 3 m were positioned adjacent to the spawning starfish. Unlike the pump array, the substrate traps were left open for the full duration of spawning. Each tray had a plastic lid to close the tray during retrieval.

Current speeds were measured using a Neil Brown acoustic vector-averaging current meter, suitable for combined wave and current environments. The current meter was supported on a bottom-mounted metal frame and manually raised and lowered to measure the vertical velocity profile. The meter failed after 3 days of experiments (up to and including Experiment No. 7) and currents on 2 subsequent days were estimated by timing the

passage of a dye cloud traveling between the starfish and the pump array. A surface-piercing capacitance probe (Black and Rosenberg, 1991) was deployed to record wave conditions at the sea surface.

To check instrument accuracy, wave probe gain and offset and current meter zero offset were calibrated in still water each day. Instrument output was logged on a portable computer at a sampling rate of 2 Hz. The current meter outputs were later averaged over 17 min (2048 data points) to find mean currents.

Collection. Prior to each experiment, searches were made to remove any crown-of-thorns starfish within the transect. A starfish of known sex was then collected and injected with 1-methyladenine to induce spawning. The females normally began spawning after 20 min, while the males usually took half that time.

Eggs or sperm were collected downstream of the starfish. The pump array used for the collections was moved to 0.5, 1.0, 3.0, and 10.0 m downstream (Fig. 1). Immediately prior to sampling, all lines were disconnected from the downstream filters and the pumps were run for 1 min to flush the hoses. The hoses were reconnected rapidly (in less than 30 s) and filtering was carried out for 2 min. Flow rates for a given pump were consistent, so the volume that passed in 2 min through each pump (about 4 l) was measured several times and averaged. While the pumps were active, dye was released next to the starfish to ensure that the array was correctly positioned downstream. All experiments were undertaken in reasonably clear and calm conditions with wind speeds of less than 10 knots, waves less than 0.5 m, and mostly slow current speeds of less than $0.1 \text{ m} \cdot \text{s}^{-1}$ (Table 1).

Filtering and counting. Eggs collected from the water column were filtered into a plastic bottle through 80- μm plankton mesh placed in a bucket of seawater. A large volume of seawater in the bottle prevented eggs being crushed or forced through the mesh as would have occurred by filtering in air. On completion of pumping, the filter was removed from the bucket, the external surface of the meshes was washed, and the eggs were trapped in the water draining into a small sample tube at the base of the plastic bottle. The small sample tube was then removed and 1 ml of formalin added to preserve the eggs. Because sperm could pass through the filters, a 20-ml subsample was collected without filtering from the 2-min pumped sample and preserved with formalin.

The contents of each substrate trap were placed in a funnel over a filter and washed with seawater to dislodge any eggs. The surface of each filter was then washed, and the eggs were collected and preserved as described above.

Eggs in each sample were counted at $25\times$ with the aid of a binocular microscope; sperm counts were made at $400\times$ using a phase contrast microscope. Subsamples of

Table 1

Information on the sex, duration of spawning, pump and trap positions, and environmental conditions pertaining to each experiment

Exp. No.	Sex	Spawning duration (min)	Pump array position (m)	Substrate trap position (m)	Currents	
					Direction	Speed ($\text{m} \cdot \text{s}^{-1}$)
1	F	25	0.5, 1, 3	0.5, 1, 3	N	0.02
2	F	20	0.5, 1	0.5, 1, 3	N	0.08
3	F	60	0.5, 1, 3, 10	0.5, 1, 3	N	0.04
4	F	45	0.5, 1	0.5, 1, 3	E	0.05
5	F	65	0.5, 1, 3, 3	0.5, 1, 3	N	0.02
6	F	50	0.5, 0.5	0.1, 0.5, 1	S	0.02
7	F	65	0.5, 1, 3, 10	0.5, 1, 3	S	0.10
8	F	35	10, 10	0.5, 1, 3	S	0.23
9	F	55	0.5, 1, 3	0.5, 1, 3	S	0.07
10	M	20	0.5, 1	—	S	0.03
11	M	20	0.5, 1	—	S	0.03
12	M	20	0.5, 1	—	S	0.03
13	F	25	10, 10	0.5, 1, 3	S	0.25
14	F	50	0.5, 1, 3	0.5, 1, 3	S	0.20
15	M	30	0.5, 1	—	S	0.03
16	M	20	0.5, 1	—	S	0.02
17	M	25	0.5, 1	—	S	0.02

water were extracted, using a pipette, from well-shaken sperm samples and drops applied to a hemacytometer. Counts were obtained from a total of five of the large squares.

Fall velocities. One of the most important factors determining the distribution of eggs or sperm in the water column is the fall velocity (or buoyancy). Because no measurements of the distribution of fall velocity for starfish eggs were available, we applied analysis techniques normally used to measure fall velocity and grain size of fine sediments.

Eggs or sperm were thoroughly mixed in a 1-l measuring cylinder. The room and water temperatures were the same to reduce convection in the cylinder. After the turbulence had ceased, 10-ml subsamples were taken at 0.05 m and at 0.1 m from the surface every 15 min for eggs and every 45 min for sperm. Eggs were sampled over a period of 2.25 h and sperm over 7.5 h. Live eggs were used in two replicate experiments. For sperm, one set was killed by exposure to formalin to test whether the motility of live sperm affected their sinking rates. Data for each gamete type were then fitted separately to a logarithmic decay curve, and estimates of the 10th percentiles were used to determine fall velocities. The temperature of the oceanic water used for these measurements was 23.8°C and the salinity was 35 ppt.

Lagrangian advection/diffusion numerical model of larval dispersal

As gametes progress downstream, they advect with the main current and diffuse due to turbulence. In this paper,

we investigate whether the movement of the eggs and sperm can be described by advection/diffusion principles more commonly applied to pollutants or sediment. To this end we adapted a Lagrangian particle model of sediment suspension under waves; this model was previously described by Black and Rosenberg (1991). The particle technique provides a number of numerical advantages; is intuitively a more direct reproduction of the natural processes; and eliminates numerical diffusion, particularly near the starfish where concentration gradients may be large.

In the Lagrangian model, several thousand particles are released with position $X(x, y, z)$ to represent the gametes. The model tracks the vertical and horizontal movement of gametes by sequentially treating the entrainment, diffusion, and then advection each time step. The unknown physical variables that had to be estimated from field data were the vertical dependence of the current $U(z)$, the eddy diffusivities (e_x , e_y and e_z), and the fall velocities.

Entrainment. Starfish eggs are generally released from openings (gonopores) that radiate from the central disk along the tops of the arms. It was estimated that starfish eggs were released from a circle approximately 0.15–0.20 m in diameter (consistent with a starfish diameter of 0.35–0.40 m). Our measurements of the initial concentrations were made 0.05–0.10 m above the starfish. In the model, entrainment was simulated by releasing particles at random initial positions within a cuboid with dimensions representative of the natural case. The length and

width of the cuboid were taken as 0.175 m and the height was 0.075 m.

The model maintained a constant concentration within the cuboid equal to the measured values. At each time step, the number of particles within the cuboid was determined and the appropriate number added to compensate for those that moved downstream.

Diffusion, advection, and concentration. In the Monte Carlo diffusion stage, all particles in the water column "jumped" horizontally or vertically with the step size ΔX_1 governed by the eddy diffusivity, where

$$\Delta X_1 = R_n(6E_s\Delta t)^{0.5} \quad (1)$$

and R_n is a random number in the uniform range $(-1, 1)$; E_s is the lateral, longitudinal, or vertical eddy diffusivity; and Δt is the time step. The factor 6 in eqn (1), rather than 2, results when a uniform random number range is chosen instead of $R_n = \pm 1$.

In the linear advection stage, each particle's vertical position was adjusted according to its fall velocity as

$$\Delta z = W\Delta t \quad (2)$$

The downstream position was adjusted according to the current speed $U(z)$ at the level of the particle (z) above the bottom

$$\Delta x = U(z)\Delta t \quad (3)$$

The concentration at any elevation was the sum of the particles lying in a vertical cell, divided by the cell volume

$$C_z = \sum_{i=1}^n N_i/(dx dy dz) \quad (4)$$

where n is the number of particles, and dx , dy , and dz are the cell dimensions.

A short time step of $\Delta t = 0.05$ s was chosen to refine the model resolution. In a Lagrangian model, the vertical grid size does not influence the solution, but is selected according to the resolution required. More particles and shorter time steps are needed to properly resolve sharp concentration gradients on fine grids.

To determine concentrations as recorded in the field, particles were tracked until they passed the downstream location of the pump array. The cumulative number of particles per liter of fluid passing through model grid cells of size $dy = dz = 0.2$ m over a 2-min interval was determined. The water volume passing through each cell was

$$V = U(z)dydz t \quad (5)$$

where t is the elapsed time (120 s). To allow an equilibrium to develop in the model (as in the field condition), the simulation ran for 80–600 s (depending on the current strength) before the summation of particle numbers was commenced. The model then ran for a further 120 s.

The velocity profile and roughness length. The vertical velocity profile was assumed to be logarithmic. Thus

$$U(z) = 5.75u_* \log_{10}(z/z_0) \quad (6)$$

where u_* is the friction velocity and z_0 is the roughness length, the height at which the velocity goes to zero. The speed at any elevation was

$$U(z) = U_m \log_{10}(z/z_0)/\log_{10}(z_m/z_0) \quad (7)$$

where U_m is the velocity measured by the current meter at elevation z_m .

Measurements of the measured velocity profile indicated z_0 was in the range 0.08–0.15 (previously reported by Black and Gay, 1990). This value is in accordance with a number of other estimates. Summarized by Black and Hatton (1990), z_0 values of approximately 0.08 m (or friction coefficients equivalent to $z_0 = 0.08$) have been independently obtained using wave height attenuation data and numerical model calibrations (Black and Gay, 1990; Hardy and Young, 1991). Thus, we have taken $z_0 = 0.08$ m in this study.

Eddy diffusivities. The current and wave measurements showed a mean circulation superimposed on an oscillating wave orbital motion. Spectra of the sea-surface time series indicated two wave trains with periods of about 8 and 3 s. The dominant 8-s peak was probably associated with swell, whereas the 3-s waves were generated by local wind.

In wave/current environments, the most common assumption is a parabolic vertical distribution of eddy diffusivity above the wave boundary layer (e.g., Fredsoe *et al.*, 1985), although more than 30 different techniques have been proposed to predict bottom shear stresses and bed roughness scales under the combined action of waves and currents (Simons *et al.*, 1989). Despite this wide choice of models, very few have been fully calibrated against the few suitable field data available.

The complexity of the available relationships varies, but Nielsen (1986) has found that the simplest case of a vertically invariant eddy diffusivity is effective for predicting suspended sediment concentrations, and this was confirmed by Black and Rosenberg (1991) after examining a series of suspended-sediment load measurements under natural waves.

In this paper, we applied a vertically invariant eddy diffusivity for $z > z_0$, and allowed the eddy diffusivity to decrease linearly to zero for $z < z_0$. The linear decrease near the bed was found to have very little effect on the model results. We used the field measurements of egg and sperm concentrations to determine the adequacy of this formulation. Although local wind creates a second boundary layer at the surface, this layer could be neglected in the model because eggs and sperm did not spread to

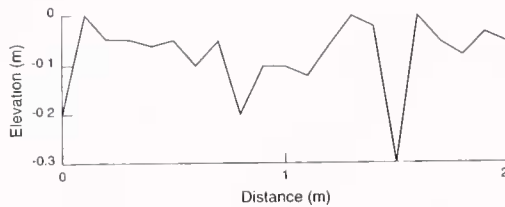


Figure 3. Seabed bathymetry over a 2-m distance at the study site, showing variations of up to 0.3 m.

the surface in significant numbers over the spatial scales considered.

Defined bed level. The velocity of all particles was set to zero in the region below “mean bed level,” *i.e.*, within one roughness length ($z_0 = 0.08$ m) of the bed where the velocity profile is undefined. Zero net current in this zone is probably a reasonable approximation because of the sheltering induced by the coral. However, because the coral is porous, some water movement may still occur, particularly when waves are present. Consequently, random movement was retained below $z = z_0$.

The lowest pumps were estimated to be about 0.3–0.4 m above the minimum bed level ($z = 0$) in the model. The pumps were 0.2 m above the base of the pump array frame while the bed profile at the study site exhibited variations of up to 0.3 m (Fig. 3), and the pump frame base was generally located on the crests of the undulations. Mean bed level is expected to be at an elevation dependent on the magnitude of the roughness length. However, the frame was moved often and there remains some uncertainty, of the order of 0.2 m, in the defined position of the bed in the field data relative to the model.

Boundary conditions. At the surface, a zero flux boundary condition was imposed by reflecting any particles that attempted to move through the surface by diffusion.

The bottom boundary condition is best described as a “settling or trapping” condition, established to investigate the entry of particles into the bed matrix. In this paper, “settlement” is used in the sediment transport sense to denote contact with the seabed. A square grid covering the seabed was established in the model with 0.13-m sides, so that the surface area of each cell was equal to the area of the substrate traps (0.0169 m²). Particles were said to have settled if their vertical position was within $0.1z_0$ of the defined bottom. Physically, this means that the particles would be well within the hollows in the bed undulations. Model tests showed that the defined level at which settlement was said to occur only marginally influenced the absolute numbers trapped when the defined level was less than z_0 . Moreover, changes to the defined settlement level had no obvious influence on the predicted pattern of settlement. Once settled, particles were eliminated from

the active pool. To record the event, a particle counter for the cell in which they settled was incremented by 1.

Results

Fall velocities of eggs and sperm

The laboratory measurements of fall velocity indicated a range of small negative buoyancies for the eggs (Fig. 4), with a median fall velocity of 0.072 mm · s⁻¹ (0.26 m · h⁻¹). The sperm were essentially neutral whether alive or dead (Fig. 4). Measured sperm concentrations, even after 7 h, remained scattered about the neutrally buoyant curve.

A best fit curve for eggs was determined of the form

$$C/C_0 = e^{-t/\tau} \quad (8)$$

where C is the concentration, C_0 is the concentration at time $t = 0$ (hours), and τ is the decay coefficient (hours). The data exhibited a correlation coefficient of $r = -0.97$ to the curve

$$C/C_0 = e^{-t/0.556} \quad (9)$$

From eqn (7), the time taken for the concentration to halve is 0.384 h, which corresponds with a fall velocity over 0.1 m depth of 0.072 mm · s⁻¹, as given above.

Although the eggs are slightly negatively buoyant, a neutral condition for both the eggs and sperm is a reasonable approximation over the spatial scales being considered. This was subsequently confirmed with the numerical model by comparing results using the measured mean fall velocity and the neutrally buoyant condition.

Dynamics of gamete release

Although there was considerable individual variation, the rate at which female crown-of-thorns starfish released eggs was generally greatest at the beginning of the spawning event and declined logarithmically with time (Fig. 5).

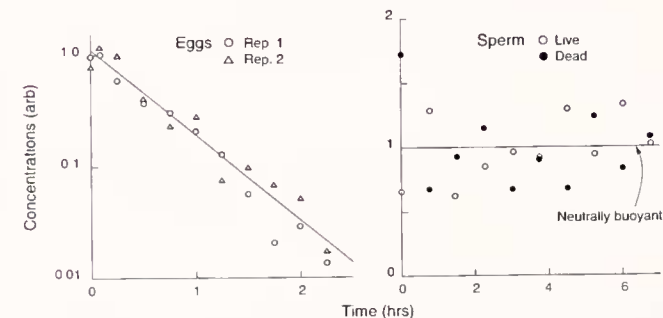


Figure 4. Egg and sperm concentrations at 0.1 m below the surface of the settling tube as a function of time. Note the close correspondence of the two replicate logarithmic plots for live eggs, and the close similarity of the plots for live and dead sperm.

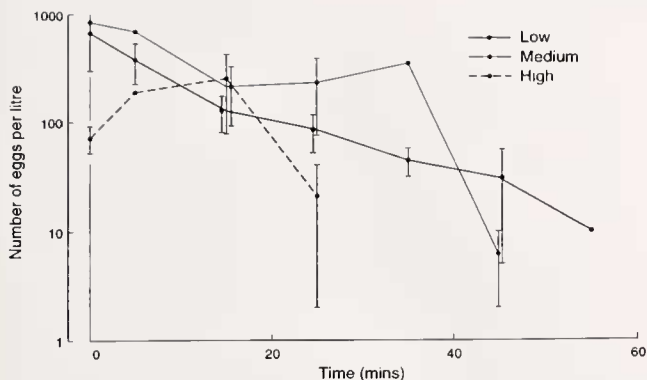


Figure 5. Temporal dynamics of egg release. Number of eggs per liter next to the spawning starfish is plotted on a logarithmic scale as a function of time since the start of spawning, for low, medium, and high current speeds.

This trend was consistent for two of the current flow regimes (low $0.02\text{--}0.05\text{ m}\cdot\text{s}^{-1}$, medium $0.07\text{--}0.10\text{ m}\cdot\text{s}^{-1}$). In high flows ($0.2\text{--}0.3\text{ m}\cdot\text{s}^{-1}$), the results were more erratic. Overall, a mean of 10^3 eggs l^{-1} was recorded close to the starfish at the start of spawning, and total production over the mean spawning period of 45 min averaged $2.0 \times 10^4\text{ eggs l}^{-1}$.

Measurements of egg concentrations adjacent to the starfish are more prone to experimental error in fast currents, particularly with respect to accurate placement of the pump near the starfish, which may explain the smaller observed number of eggs at $t = 0$ during high flows (Fig. 5). In addition, as noted above, the number of eggs released by individual starfish varies considerably.

The rate at which individual male starfish released sperm varied considerably, but no decline in the rate of

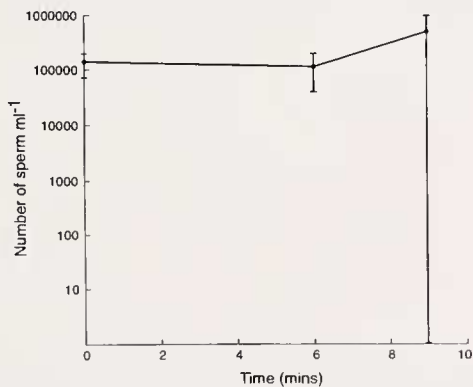


Figure 6. Temporal dynamics of sperm release. Number of sperm per milliliter next to the spawning starfish is plotted on a logarithmic scale as a function of time since the start of spawning. Data were available only for slow currents and for up to 10 min from the start of spawning.

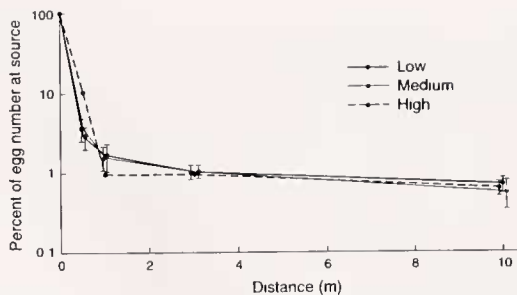


Figure 7. Egg dispersion. Logarithmic plot of eggs per liter as a function of distance from the spawning starfish, for low, medium, and high currents, expressed as a percentage of the number of eggs per liter at the spawning starfish.

release was observed during the first 10 min after the start of spawning at low current flows, the period and conditions for which data were available (Fig. 6). A mean of $10^5\text{ sperm ml}^{-1}$ was recorded close to the starfish at the start of spawning, and total production over the mean spawning period of 10 min averaged 2×10^9 . The concentration near the starfish of 10^5 is much less than the concentrations of $8 \times 10^8\text{ sperm ml}^{-1}$ recorded by Benzie and Dixon (1994) in the laboratory. The reduction is indicative of the initial dilutions occurring immediately adjacent to the starfish.

The total of 10^9 sperm is equivalent to a volume of concentrated sperm in the testes of approximately 50 ml (calculated from data in Benzie and Dixon, 1994), and suggests a rate of sperm release of $3 \times 10^6\text{ sperm s}^{-1}$.

Downstream gamete concentrations

Average egg concentrations, calculated as the mean number of eggs per liter over all pumps with non-zero values, fell rapidly with increasing distance from the spawning adult (Fig. 7). By a distance of 1 m, egg concentrations fell to one hundredth of that near the starfish, taking until 10 m before approximately halving in value again (Table II). Current strength does not strongly affect

Table II

Average concentrations of eggs measured on the frame (as a percentage of the concentration at the starfish) for slow, medium, and fast currents

	Distance downstream (m)			
	0.5	1.0	3.0	10.0
Slow	3.3	2.4	1.5	0.8
Medium	2.2	0.7	0.2	0.3
Fast	10.0	1.0	1.0	0.7

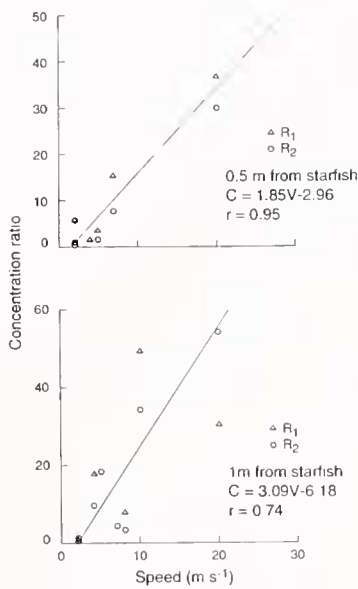


Figure 8. Vertical spread of eggs and sperm. The ratio of egg concentrations for the five pumps on the lowest level and the five pumps on the next highest level (Fig. 2) are plotted against the current speed. R_1 is the ratio of average concentrations, and R_2 is the ratio of maximum concentrations in each level.

the downstream concentration after normalizing by the concentration recorded near the starfish (Fig. 7).

To examine the spread of the gametes as a function of the current strengths, the following two ratios were determined:

$$R_1 = C_{av0}/C_{av1}; \quad R_2 = C_{max0}/C_{max1} \quad (10)$$

C_{av0} and C_{av1} are the averages of the concentrations measured across the lowest level and the next lowest level of the frame respectively (450 mm apart; Fig. 2). C_{max0} and C_{max1} are the maximum concentrations measured in the same two rows. These ratios indicate whether the gametes spread evenly through the water column or favor the lower or upper level. R_1 and R_2 are both correlated with current strength at 0.5, 1.0, and 3.0 m from the starfish (Fig. 8). This means that the eggs are found closer to the bottom as the current strength increases over these space scales (see also Figure 11, low and medium current case).

At 10 m, egg concentrations were lower near the bed than at the higher levels (Fig. 11). This may be caused by substrate trapping of the near-bed particles (see below) or velocity shear. By acting as a sink, substrate trapping reduces the number of eggs near the bed. The effect of current shear was depicted by dye released near a starfish in slow currents. The dye was observed to spread between the bed and the surface after about 3 min, but the dye in the upper levels reached the downstream location fastest. This can result in higher concentrations in the upper levels

in the period before the arrival of the slower moving dye near the bed.

Due to variations in gamete release rates in different starfish, the data do not permit further analysis of the absolute concentrations (without normalizing) as a function of current strength. However, modeling of the spatial distribution of eggs in the pump array described in a later section demonstrated clear differences in the dispersion of the gamete cloud at different current speeds and was in accordance with the field measurements (Fig. 11).

Data for sperm were limited to within 1 m of the spawning male because of the practical difficulties of adequately sampling sperm at greater dilutions. The percentages of sperm at 0.5 and 1.0 m are very similar to those for eggs (Fig. 9). This important result indicates that both are influenced by the hydrodynamics in the same way, and are not showing any major differences in their response as a result of factors such as their size or buoyancy. Sperm concentrations near the starfish (10^5 sperm ml^{-1}) fell to approximately 10^3 sperm ml^{-1} by 1 m.

Bed settlement

An average of 0.007% of the total number of eggs produced over a spawning entered the substrate (Fig. 10). Most did so near the spawning female, at densities up to 6000 eggs m^{-2} . Patterns of settlement into the seabed differed between current speeds (Fig. 10). The proportion of eggs entering the substrate was greater, and the majority settled closer to the starfish, for the slowest currents. At high current speeds few eggs entered the substrate traps, and did so only at some distance from the female.

Model simulations

Three field cases were modeled to encompass a range of current speeds and to provide a complete calibration, verification, and validation sequence over a wide range

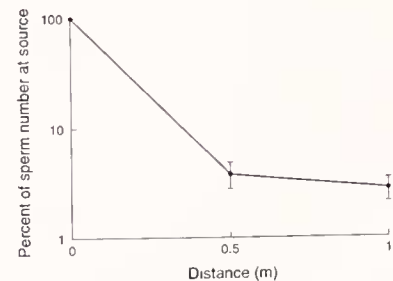


Figure 9. Sperm dispersion. Logarithmic plot of sperm per milliliter as a function of distance from the spawning starfish, expressed as a percentage of the number of sperm per milliliter at the spawning starfish. Data were available only for slow currents and for up to 1 m from the spawning starfish.

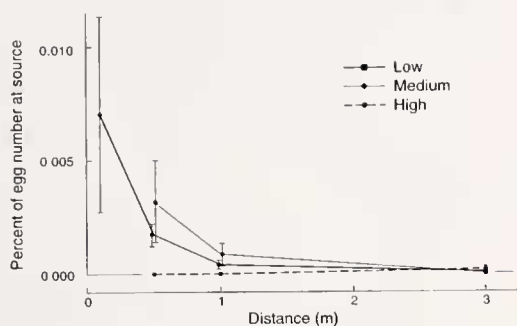


Figure 10. The proportion of the total number of eggs per liter that were produced near the spawning starfish over the course of an experiment and entered the substrate traps at different distances up to 3 m from the starfish, for low, medium, and high current speeds.

of current conditions. The first, Case 1, examined a very slow current ($0.02 \text{ m} \cdot \text{s}^{-1}$) with the pumps 1 m from the starfish; it was compared with data from Experiment No. 1 (Table I). The second, Case 2, was a simulation over 1 m when the current was faster ($0.07 \text{ m} \cdot \text{s}^{-1}$); it was compared with data from Experiment No. 9 (Table I). The third simulation, Case 3, examined dispersal at larger spatial scales and fast current speeds (*ca.* $0.25 \text{ m} \cdot \text{s}^{-1}$); it was compared with two sets of field measurements (made sequentially for replication) during Experiment Nos. 13 and 14 (Table I).

We applied eddy diffusivity values in the range $0.0005\text{--}0.0015 \text{ m}^2 \cdot \text{s}^{-1}$. Although the tests were not exhaustive, we chose $0.0015 \text{ m}^2 \cdot \text{s}^{-1}$ for all three directions. This compares favorably with the value of $e_z = 0.0012 \text{ m}^2 \cdot \text{s}^{-1}$ found by Black and Rosenberg (1991) in a wave-driven environment, although the horizontal values were smaller than expected (Elder, 1959). The results proved to be sensitive to the choice of eddy diffusivity, but we were unable to distinguish any need for an eddy diffusivity that depended on current strength.

Comparison of model with data. The measurements and model show a clear correspondence in all three cases (Fig. 11). In particular, the spread of the cloud, the spacing of the contours, their absolute magnitude, and their vertical position in the water column are in good agreement. The tendency for the gametes to stay near the seabed is evident in both the model and the measurements. Indeed, the magnitude of deviations between the measurements and the model is less than the variability in the concentrations measured at the starfish, which is a determining input to the model, and is within the variation between replicates. For example, in Case 1, when the current (U) was only $0.02 \text{ m} \cdot \text{s}^{-1}$, the larvae spread over a greater depth and spread more horizontally than in Case 2 ($U = 0.07 \text{ m} \cdot \text{s}^{-1}$). This is depicted by the measurements and the model. In Case 3, when the currents were very fast (U

$= 0.25 \text{ m} \cdot \text{s}^{-1}$), the tendency for the gametes to be found only at the lower levels is exhibited in the model. Also, the magnitude of the predicted concentrations lies within the variability exhibited by the two sequential sets of field measurements (Fig. 11, Case 3). Notably, the horizontal offset between the two sets of field measurements and the model relates only to the positioning of the frame relative to the gamete cloud in the field.

The values of the horizontal eddy diffusivities are supported by the model calibration. In a series of sensitivity simulations, it was found that larger values tended to overly spread the gamete cloud laterally in the model.

Less well predicted is the measured tendency for egg concentrations to be very small near the seabed at distances greater than 10 m (Fig. 11). However, simulations carried out over 60 m and 100 m did exhibit lower concentrations near the bed. In addition, egg numbers decreased near the bed at 10 m in the model due to the losses associated with substrate trapping (Fig. 12). The egg concentrations (rather than egg numbers) in the model remained high because the water volumes predicted to pass through the frame at the low levels were small, in accordance with the small currents in the logarithmic boundary layer. Thus, some refinement of the behavior at near-bed levels may be required.

In general, although the model is far simpler than nature, it appears to contain the essential physics needed to address questions about the dispersal of eggs and sperm. The reduction in concentration with distance from the starfish is evidently being effectively predicted. Moreover, the assumptions made about the shape of the velocity profile and the eddy diffusivity appear to be adequate. The results indicate that the starfish eggs and the much smaller sperm can be treated as passive particles at these temporal and spatial scales.

Models of egg dispersal. The pattern of gamete dispersal in each of the current classes is clearly demonstrated in the diagrams showing egg clouds in both plan (top) view and in cross-section (side view) at the end of the simulation of Cases 1, 2, and 3 (Fig. 13). This is 3.5 min after the first release of eggs. In Case 1, the particles spread throughout the depth. This concurs with field observations in which dye spread between the bed and the surface after about 3 min.

In Case 2, when the current was $0.07 \text{ m} \cdot \text{s}^{-1}$, the eggs spread through about one third of the depth only. Indeed, in Case 3, when the current was $0.25 \text{ m} \cdot \text{s}^{-1}$, the eggs remained in the lower half of the water column after 10 m.

Two opposed factors determine the downstream concentrations of eggs and sperm. First, for a given release rate, the concentration of eggs near the starfish will be a function of the current speed, which determines the initial dilution. That is, if eggs are transported away quickly, the

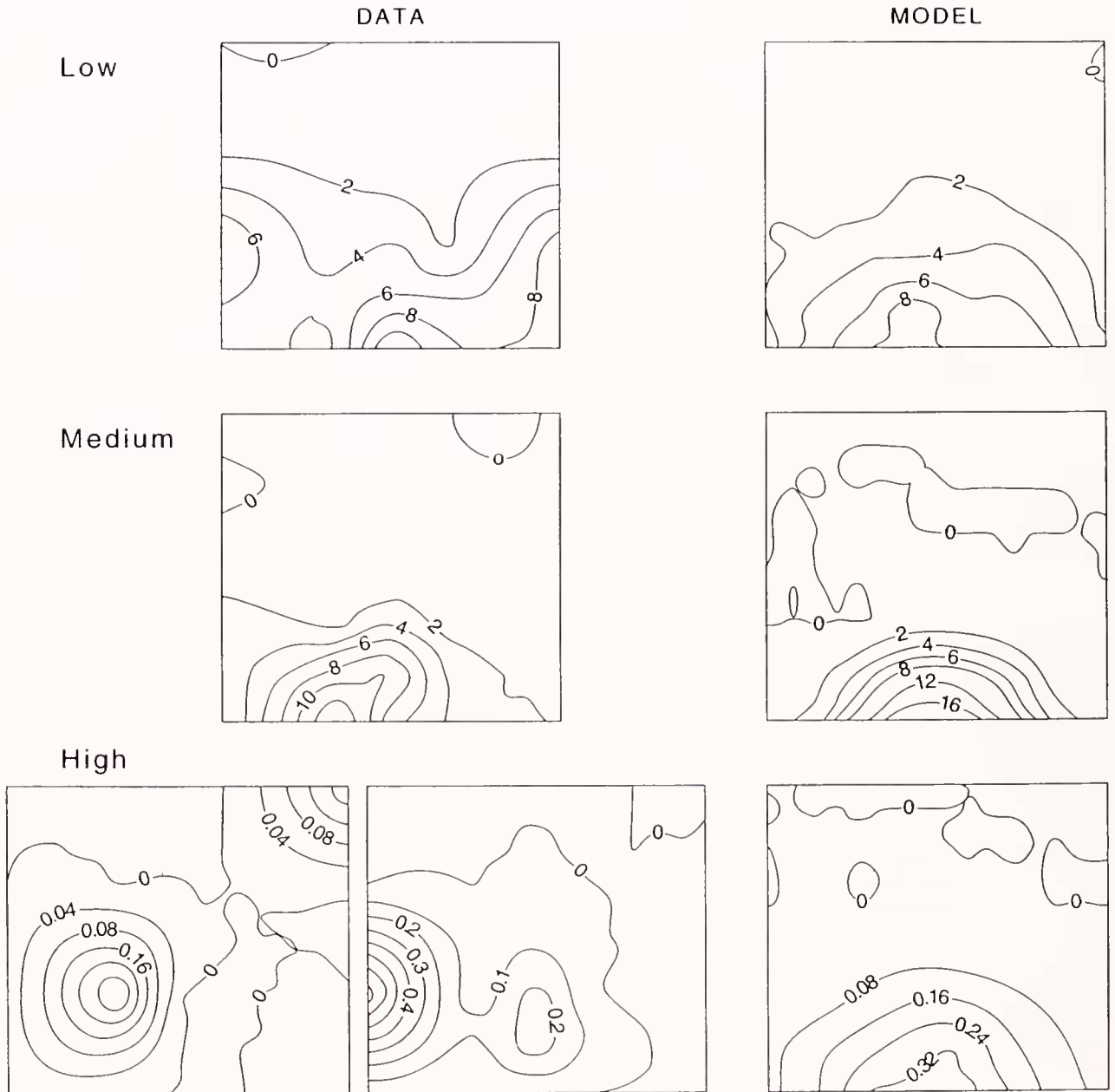


Figure 11. Comparison of measured egg concentrations (eggs per liter) with those predicted from the model for three different cases, representing an example from one each of low ($0.02 \text{ m} \cdot \text{s}^{-1}$ at 1 m distance from the spawning starfish), medium ($0.07 \text{ m} \cdot \text{s}^{-1}$ at 1 m distance), and high ($0.25 \text{ m} \cdot \text{s}^{-1}$ at 10 m distance) speed currents. The horizontal offset between measurements and data relates only to the position of the pump array relative to the egg cloud, and does not indicate any fundamental difference between the model and measurements. In fact, not only is the general fit in dispersion pattern good, the concentrations generated in the model are very close to those measured.

concentration in a region near the starfish will be reduced. The measurements and model also show that the vertical spread of the gametes is less over a given downstream distance in fast currents, which compensates in part for the higher initial dilution. Indeed, Figure 7 indicates that

the downstream concentrations normalized by the concentration at the starfish are not a strong function of current strength, even though the ratio of downstream concentrations at different depths indicated that gametes remained closer to the bed in fast flows. The measurements

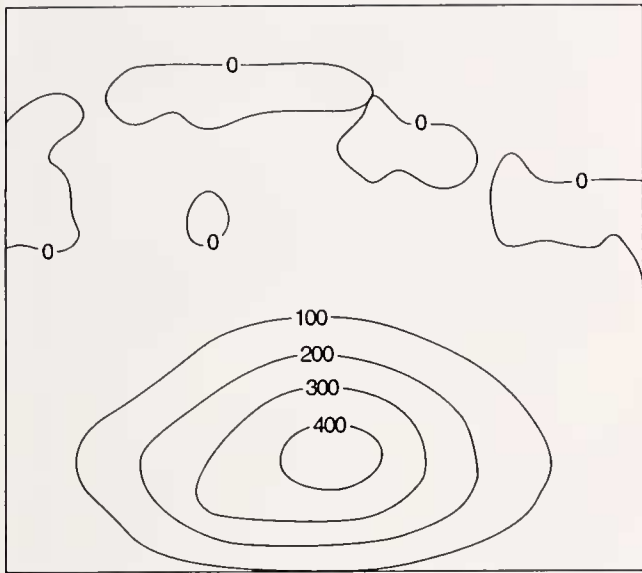


Figure 12. Egg numbers predicted by the numerical model, showing a reduction near the seabed due to substrate trapping at 10 m from the starfish in currents of $0.20 \text{ m} \cdot \text{s}^{-1}$.

did not indicate a need for an adjustment to the eddy diffusivity as a function of current speed over the range of speed and space scales considered.

The predicted contours of the number of eggs trapped in the seabed for the simulation of Cases 1–3 indicate that, if the starfish spawned in the hollows of the undulations, many of the eggs would be trapped nearby (Fig. 14). The model predicts that hundreds of eggs per 0.0169 m^2 (the size of our settlement dishes) enter the seabed. This is higher than the field measurements, but similar numbers were recorded in one case (Experiment No. 4) when up to 118 eggs were trapped at 0.5 m downstream of the starfish. The traps were very shallow (about 0.05 m) and may not have retained all of the settling eggs. Moreover, the entrances of some bed settlement traps were above mean bed level. At this level, the influence of local hydrodynamics, including wave orbital motion creating currents within the dish, was not known.

Discussion

Inferred fertilization success

A rapid reduction in concentration was measured with increasing distance from spawning crown-of-thorns starfish. These concentrations do not, however, necessarily indicate the levels of fertilization to be expected for the species, even though their rate of decline was similar to the decline in fertilization success reported for sea urchins (Pennington, 1985; Levitan *et al.*, 1991) and ascidians

(Grosberg, 1991). In those studies, fertilization success dropped dramatically—from 80 to 100% near the spawning male to about 10% or less over 1 m—and the authors inferred gamete dilution to be the significant factor contributing to the observed decline. Unlike the present study, none of these previous studies measured the field concentrations of the gametes.

To infer fertilization rates from gamete concentrations, we used data obtained from mixing gametes of crown-of-thorns starfish at different concentrations in the laboratory (Benzie and Dixon, 1994). These calculations were based on the mean concentration of sperm observed in the field and on fertilization data from both early and late in the breeding season. Benzie and Dixon (1994) showed that gamete quality, and hence fertilization success, varied according to the time of the breeding season.

If we assume that the diluted sperm pass across a downstream spawning female, the calculations suggested the following rates of fertilization if spawning occurred early in the breeding season: 100% with the female adjacent to the male, 90–100% at 1 m, 90–100% at 3 m, and 70–100% at 10 m. Towards the end of the season the rates of fertilization were estimated as 90% near the male, 80–90% at 1 m, 75–80% at 3 m, and 60–70% at 10 m. These results are consistent with the published fertilization rates of 80–90% at 1 m and 60–70% at 10 m for crown-

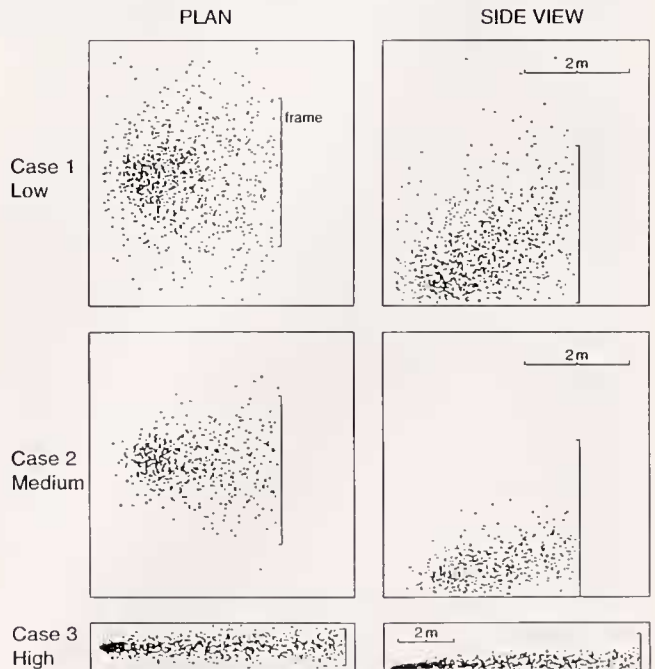


Figure 13. Position of the egg cloud in plan (top) view and cross-section (side view) after 3.5 min of simulation in Cases 1–3, representing one example from each of low, medium, and high speed currents.

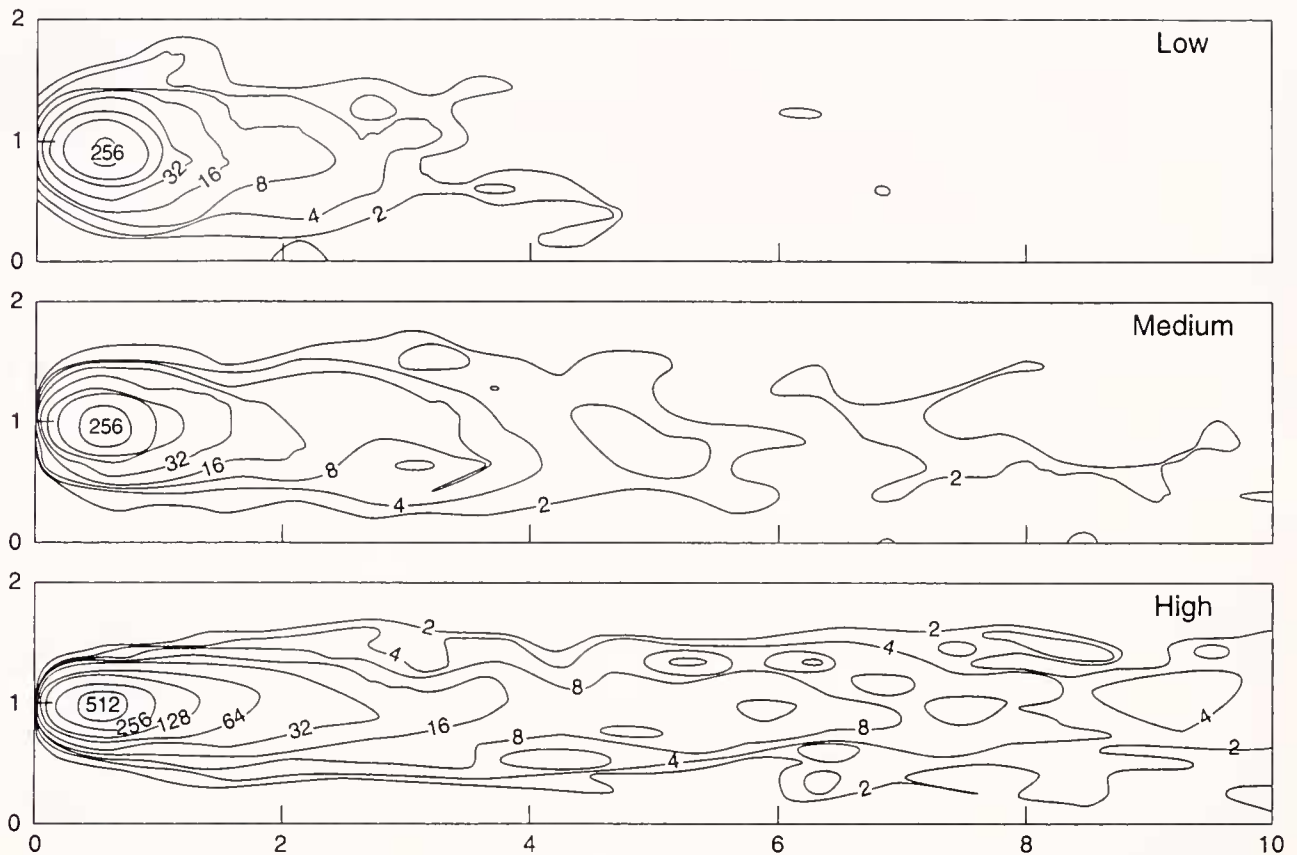


Figure 14. Number of eggs predicted to enter the seabed for each of the Cases 1–3. These cases provide one example from each of low, medium, and high current speeds. The model was run until the eggs had reached the 10-m mark, and then egg numbers were allowed to accumulate for 2 min.

of-thorns starfish in the field (Babcock and Mundy, 1992, 1993).

These fertilization rates are far higher than those observed for sea urchins, and it has been suggested that this is because the crown-of-thorns starfish is far more fecund than other echinoderms (Babcock and Mundy, 1992; Babcock *et al.*, 1993). The measured concentration of the starfish sperm, of approximately 10^5 sperm ml^{-1} near the spawning male in the field, suggested rates of sperm release of 3×10^6 sperm s^{-1} . These data compare well with the rates of sperm release of 10^5 – 10^6 s^{-1} calculated by Benzie and Dixon (1994) from laboratory measurements, and are similar to the rates of release for sea urchins of 1 – 3×10^6 sperm s^{-1} calculated by Denny and Shibata (1989). Therefore, assuming similar rates of sperm release and similar dispersion patterns in given flow regimes, sperm concentrations for sea urchins at 1 m downstream from the spawning male would be equivalent to those measured for crown-of-thorns starfish (10^3 sperm ml^{-1}).

Fertilization rates expected from such sperm densities, using Figures 1 and 2 from Levitan *et al.* (1991), range

from 5 to 30%. This is within the range of field measurements (for fast current speeds and slow currents speeds) made by Pennington (1985). Such measurements have used either samples of large numbers of eggs in syringes (Pennington, 1985) or samples of eggs taken from spawning females set downstream of a male (Babcock and Mundy, 1992; Babcock *et al.*, 1993).

The higher field fertilization rates of crown-of-thorns starfish, relative to sea urchins, therefore reflects the higher fertilizing capacity of starfish sperm at a given dilution, as observed in the laboratory by Benzie and Dixon (1994). The fertilization is evidently not due to a higher production of gametes as suggested by Babcock and Mundy (1992), who used sperm release rates of 4 – 8×10^8 sperm s^{-1} to explain the high fertilization rates in the field. The production of far higher numbers of eggs by crown-of-thorns starfish may still increase the overall numbers of fertilized zygotes produced, but the fecundity of the starfish does not appear to influence rates of fertilization (through increasing gamete concentrations) in the field.

The basic advection models used in this study adequately predicted the distribution of eggs and sperm of crown-of-thorns starfish in the field. Given this, they can be used to predict with some confidence the dispersion patterns of crown-of-thorns gametes over greater spatial scales and for a greater variety of hydrodynamic conditions. Using laboratory data on fertilization rates, average fertilization expected in the gamete cloud at 100 m downstream from a spawning male at currents of $0.25 \text{ m} \cdot \text{s}^{-1}$ was 25% (range 0–50%). These are very similar to the rates published by Babcock and Mundy (1992) and Babcock *et al.* (1993).

Local substrate settlement

Although small in proportion (0.007%), a significant number of eggs were entrained in the substrate. Most of these entered the substrate near the spawning female at low-medium currents. At high currents, eggs were detected only in the substrate traps at 3 m. These results may explain why the starfish often mount high coral heads to spawn. The elevated position puts the eggs into the water column away from the seabed, maximizing the chance of long-range dispersal. Coral reefs have a high roughness value, and Eckman (1990) found that the rates of settlement should increase monotonically with aerial density of roughness features.

The small-scale hydrodynamics around the substrate traps could not be assessed, but flow patterns in the vicinity of similar collection devices (Gardner, 1980; Butman, 1989; Yund 1991) can vary widely and may reduce capture efficiency under certain conditions. The capture efficiency of the traps used in the present study may also have been reduced by their relatively low sides (0.05 m). Consequently, it is possible that the number of eggs entering the seabed was underestimated, thereby explaining the difference between the measured and model results. In addition, the assumptions made in the model for conditions very near the bed may need further refinement.

The biological significance of egg entrainment to the seabed is not clear. If fertilized, the eggs could complete their larval development within such an environment. Their survivorship, however, is open to question because they may suffer greater mortality due to the effects of benthic predators and physical disturbance (*e.g.*, wave action). The effects of these factors may in turn be offset by the increased availability of nutritional sources. Recent research (Hoegh-Guldberg, pers. comm.) has shown that concentrations of dissolved free amino acids (DFAA), which are an important source of nutrition for larvae of crown-of-thorns starfish, are much higher in the vicinity of the coral substrate. Entrapment of significant numbers of larvae amongst such substrates may provide a mechanism for self-recruitment to the adult population.

Indirect evidence to support the occurrence of this type of phenomenon has been recorded in the field. Moran *et al.* (1985) found many small starfish 1–2 years after large numbers of adult starfish were observed in the same area. Similar events were reported almost 2 years later along the leeward side of the reef (Bell, pers. comm.) and in the north bay of Pelorus Island (Kettle, pers. comm.). Self-recruitment has been reported for other organisms. For example, McShane *et al.* (1988) found that successful recruits of the abalone *Haliotis rubra* were those that remained near the parent in the crannies of reefs on exposed coasts. Comparisons with the larvae of crown-of-thorns starfish are questionable, however, because the larval life of *H. rubra* is 7 days instead of the average 10–16 days for the starfish.

Buoyancy and natural turbulence

Results from the present study also confirmed, contrary to the assumptions of Wolanski and Hamner (1988), that the gametes of the starfish can be treated as passive, weightless particles at the temporal and spatial scales over which our measurements were taken. The fall velocities were much less than the turbulent vertical and horizontal velocities indicated by the eddy diffusivities applied in the model. Although 10% of the eggs remained in suspension after an hour in still water, the percentage would be much higher under more turbulent field conditions if some gametes were resuspended after contacting the bed. Indeed, the most important factor determining gamete numbers remaining in the water column at longer time scales may be the tendency for trapping near the seabed.

The model results, at 10 m from a spawning starfish, indicated a reduction in the number of eggs near the bed, as also measured in the field. We think this is due to the entrapment of gametes in the substrate. In a turbulent environment that mixes the gametes through the vertical, this reduction in concentration would be expected to continue with time. As such, although the eggs and sperm are neutrally buoyant, turbulence brings the gametes into the sphere of influence of the seabed and the potential exists for these to enter into cavities within the substrate. This mechanism could considerably shorten the time that larvae of crown-of-thorns starfish spend in the water column and hence their average excursions during the pelagic phase.

Numerically, for neutrally buoyant material, this trapping process is equivalent to a bottom boundary condition that allows random turbulence to carry particles into the seabed. In sediment-transport models such as the one presented by Black and Rosenberg (1991), the bottom boundary condition (described as a pick-up function) precludes this loss of particles to the bed by random dif-

fusion. The sediment particles "settle" to the seabed only when the fall velocity carries them there. Thus, the data presented in this paper provide some new insight into the dynamics very near the bed. The results suggest that random turbulence over these very rough beds may "inject" eggs and sperm into the seabed, where they remain. In fact, for neutrally buoyant material, seabed trapping (or any form of "settlement") cannot occur if random turbulent movement into the bed is forbidden in the model. The bottom boundary in this case may be described as a "trapping condition." Physically, the gametes may be trapped by snagging or attaching to the substrate.

Summary

In summary, hydrodynamics plays an important role in determining the fertilization success and recruitment of the crown-of-thorns starfish. Denny and Shibata (1989) emphasized the relationship between hydrodynamics and fertilization success, although they did not have accurate measurements of the physical environment. The present study has demonstrated the close relationship that exists between the physical characteristics of the fluid medium into which the gametes are released and their patterns of dispersal in the field.

The high fertilization rates previously reported for the crown-of-thorns starfish have been confirmed from calculations based on the gamete concentrations found in the field and the fertilization rates seen in the laboratory at those concentrations. These high rates of fertilization probably reflect the higher fertilizing capacity of the starfish sperm rather than an increase in the rate of gamete release leading to a higher number of sperm per unit volume of seawater.

The present study has also demonstrated the importance of hydrodynamics in the recruitment process. This was stressed previously by Butman (1989), who showed that invertebrate larvae can be passively deposited over large spatial scales. Our results indicate that hydrodynamics may also influence recruitment over much smaller scales—through the entrapment of gametes in the substrate. This mechanism for self-recruitment may be important in the onset of primary outbreaks of the crown-of-thorns starfish.

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